MOLTING PHENOLOGY OF HARBOR SEALS ON TUGIDAK ISLAND, ALASKA

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ABSTRACT

We documented the progression and timing of the annual molt of harbor seals by cohort (i.e., yearling, subadult, adult female, and adult male) on Tugidak Island, Alaska, from 1997 to 1999. We characterized molt categories as pre molt, active molt, and post molt. In all years, the timing of the pre molt and active molt differed among all cohorts, whereas timing of the post molt differed among all cohorts except subadults and yearlings in 1997 and 1998. Yearlings began molting first, followed by subadults, then by adult females, and lastly adult males. The timing of the active molt was similar among all cohorts in 1997 and 1998, whereas in 1999 molting occurred 3-6 days later for all cohorts except yearlings. The number of seals hauled out was, in general, positively related to the proportion of seals in the active molt and negatively related to the post molt. The precise timing of molting is not known for most areas in Alaska; thus, knowledge of the spatial variation in the timing of molting and the differences in timing among cohorts, should be considered in determining optimal survey designs for population abundance and trend estimates.

Keywords: harbor seal, *Phoca vitulina richardsi*, molting, Alaska, cohort, population estimates

INTRODUCTION

Harbor seals (*Phoca vitulina richardsi*) undergo an annual cycle of regeneration and shedding, or molting, of hair. Follicular regeneration occurs 3-6 weeks prior to any visible signs of shedding in studies of captive individuals (Montagna and Harrison 1957, Ashwell-Erickson *et al*. 1986). Shedding in adults generally occurs after the pupping and mating periods (Scheffer and Slipp 1944, Stutz 1967, Ling 1972), but prior to implantation of the embryo in females (Bishop 1967, Boulva and McLaren 1979). Harbor seal pups molt first (*in utero* before birth; Scheffer and Slipp 1944, Boulva and McLaren 1979), yearlings second (Bishop 1967, Thompson and Rothery 1987), followed by older seals (Thompson and Rothery 1987).

Sex and reproductive status ultimately determine the timing of molting, although other influential factors may include body condition, temperature, photoperiod, and hormones (Ebling and Hale 1970, Ling 1970, Riviere *et al*. 1977, Ashwell-Erickson *et al*. 1986, Gardiner *et al*. 1999). The energetic demands of molting in adult females must be balanced with the energetic demands of parturition, lactation, and mating. Molting in adult males is affected by reproductive status as hair

growth is inhibited by testosterone (Mohn 1958), which presumably declines after the mating period. Poor body condition as a result of mating behavior (Coltman *et al*. 1997) may also influence the timing of molting. Immature seals do not experience energetic demands associated with reproduction.

Seals haul out (emerge from the water to lie on land or ice) more frequently and for longer periods when molting, presumably due to higher energetic demands associated with follicular regeneration (Feltz and Fay 1966, Stewart and Yochem 1984, Calambokidis *et al*. 1987, Thompson *et al*. 1989, Watts 1992, Boily 1995, Watts 1996). The period of hair loss and regeneration may last six weeks to several months (Montagna and Harrison 1957, Ashwell-Erickson *et al*. 1986) and it is unknown if and/or when during this period the number of seals on shore is greatest. In Alaska, harbor seal population abundance and trend estimates are calculated from counts of seals obtained during aerial surveys; these surveys are conducted during mid to late August when the largest numbers of seals are assumed to be hauled out during a peak in the molting period. However, the precise timing of molting in Alaska has not been documented. Detailed data on the timing of molting and when the greatest number of seals are hauled out would be beneficial for determining optimal survey designs to estimate population size and trend (Adkison *et al*. 2001*)*. Additionally, cohort differences in the timing of molting may affect the number of seals on shore during a given time period and should be considered when determining optimal survey design.

We studied the molting phenology of a wild population of harbor seals on Tugidak Island, Alaska. The objectives of this study were to 1) categorically divide the molting period into discrete stages, 2) document the timing of molting for yearlings, subadults, adult females, and adult males, 3) determine if timing of molting varies among years, and 4) determine the relationship between seal counts and our categorical stages of molting progression.

STUDY AREA AND METHODS

We surveyed harbor seals on the southern and western shores of Tugidak Island (56°30'N, 154°40'W), 40 kilometers southwest of Kodiak Island in the western Gulf of Alaska (Figure 1) from July - September in 1997, 1998, and 1999. We used spotting scopes (15 - 60x) and binoculars (10 x 42) from atop 30-meter bluffs to categorize seals by sex, age class, and molt stage (described below).

Sex was determined by the location of genitalia when the ventrum was visible or by association of a mother and pup in July. When sex could not be ascertained, the sex was recorded as unknown. The adult seals in the unknown category were distributed to the male and female categories based on the proportion of sexed adult seals in each molt stage.

We classified seals as pups, yearlings, subadults, or adults. Pups were identified by their small size, association with their mother prior to weaning, and their new pelage with distinct spots and rings in June and July. Yearlings were defined as the smallest size class excluding pups and had a bleached pelage that lacked obvious spots and rings prior to molting. By the time most yearlings had molted (mid August), we were able to distinguish between pups and yearlings by the increasingly worn and faded appearance of the pups' pelage. We had difficulty distinguishing between pups and yearlings that were wet and so recorded these seals as unknown; this category comprised a small percent of the total; on average 21% in 1997, 12% in 1998, and 1% in 1999. In 1998 and 1999, seals in the unknown yearling or pup category were classified into three subcategories: probable yearling, probable pup, and undetermined. We used the daily ratio of probable pups to probable yearlings (and assumed that we classified an equal proportion of each into

the undetermined subcategory) to estimate the number of yearlings in the undetermined subcategory. The total yearling count was then estimated by the sum of the known, probable, and undetermined yearling categories.

The subjective division of subadult and adult age classes was based on a combination of relative size of the seal, presence of fresh wounds or scarring in the neck region, and comparison with seals of known age. For example, in July we classified a female as a subadult if she was smaller than the smallest females attending pups yet larger than yearlings. Smaller males with little or no scarring or bloody wounds in the neck region were also classified as subadults (Thompson and Rothery 1987). We confirmed our aging criterion to be reliable through observations of known aged individuals, and although some overlap in sizes between subadults and adults likely occurred, data were collected consistently by the same observers throughout each summer.

We classified seals into one of seven progressive molt stages (*a-g*) that we could visually identify (Table 1). We combined these stages into three broad categories for analysis: (1) pre molt, old hair is still present with no visible hair loss or new hair growth; (2) active molt, old hair is being shed and new hair is visible; and (3) post molt, all old hair has been shed and the seal has a completely new pelage.

Statistical Analysis

Cohort differences in timing of molting

We calculated the proportion of seals in each cohort in the pre, active, and post molt categories for each survey day; analyses were conducted separately for each molt category. Only stages *b* and *c* were used in analysis of the pre molt data; molt stage *a* was not included because it encompasses a large period of time relative to the other more distinct molt stages. We used randomization (Manly 1991) to do pairwise comparisons of the timing of molting among cohorts within years. Our test statistic, C, for comparing similarity between any two cohorts was:

$$C = \sum_i | p_{1i} - p_{2i} |$$

where i represents the sample day, p_1 is the proportion in a molt category for group 1 (*e.g.*, yearlings) and p_2 is the proportion in the same molt category for group 2 (*e.g.*, subadults). To determine whether an observed C (C_0) for any comparison was larger than expected by chance, we compared the result to a randomization distribution; i.e., we randomly assigned individual seals to the 2 groups being compared, maintaining the group total for each day. We then computed the proportion in the molt category of interest and computed C_r, where r represents the rth randomization. This procedure was repeated 9,999 times. The probability of getting C larger than C_0 was calculated by placing C_0 in its rank order among the C_r's from the randomized samples. We rejected the hypothesis of no differences in timing of molting between two cohorts being compared for large values of C_0 relative to the randomization distribution; i.e., C_0 in the upper 5% of the randomization distribution.

Variation in timing of the active molt across years

We used non-linear least squares to fit a normal curve to the observed proportions of seals in the active molt over time. We used the active molt to compare across years since we did not observe the complete post molt for adult males or the complete pre molt for yearlings and subadults. For each cohort, we used a model with separate curves for each of the 3 years. We then fit a simpler model that used the same curve for all years. If the simpler model fit the data as well as the more complex one, we concluded that there were no important differences in the timing of molting among years. Estimates of the date of the peak proportion of seals in the active molt and the differences in

peaks between years, along with standard errors and approximate confidence intervals for these quantities, were obtained directly from the curve-fitting procedure.

Relationship between seal counts and molt stage

We used simple linear regression and analysis of covariance (ANCOVA) to investigate the relationship between the proportion of seals within the various molt stages and cohort counts. For each cohort, the proportion in each molt stage (*a-g*) was computed. These proportions were used as explanatory variables in predicting seal counts; year was used as a categorical variable in the ANCOVAs to compare regression lines among years (within cohorts). Counts were the total number of seals counted in a cohort on each day, including those not classified to a molt stage; we assumed that unclassified seals had the same distribution among the molt stages as those that were classified.

RESULTS

We conducted surveys during July – September on 22 days in 1997, 27 days in 1998, and 22 days in 1999. We classified an average of 854 seals (range 412 – 1,269) per survey day.

Molting Progression

Shedding of old hair, followed immediately by visible new hair, began on the face, neck, flippers, and body openings (anus, urogenital). Shedding progressed along the ventral midline and outward over the ventrum, then along the dorsal midline, and over the dorsum. The final areas to shed were the two patches on the dorso-lateral sides of the seal. The general molting progression we observed was similar to patterns described by Stutz (1967), Ashwell-Erickson *et al*. (1986), and Moss (1992). Additionally, we found that the navel and areas of scarred tissues were among the first areas to shed. Molting yearlings and subadults appeared to follow this progression most closely while older seals exhibited greater individual variation. We also observed several cases for all cohorts where reverse molting patterns occurred; *i.e.* the last areas to shed were the head and flippers, which normally shed first.

Cohort differences in timing of molting

The timing of the pre molt and active molt periods was different (*P*<0.0001) among all cohort comparisons for each year (Figure 2). The timing of the post molt for yearlings and subadults did not differ in 1997 (*P*=0.11) or in 1998 (*P*=0.06) but did differ in 1999 (*P*<0.0001). The timing of the post molt differed (*P*<0.0001) for all other cohort comparisons. The molting patterns indicated that yearlings began molting first, followed by subadults, adult females, and lastly adult males; this molting sequence was consistent in all three years.

Variation in timing of molting across years

Overall, within each cohort, we found that the timing of the active molt varied little among years and ranged from 2 Aug (yearlings) – 2 September (adult males) (Table 2). The estimated date when the highest proportion of each cohort was in the active molt was nearly identical between 1997 and 1998. In 1999, however, the date when the peak proportion of subadults, adult females, and adult males were in the active molt occurred 3-6 days later than in the previous two years. The

estimated date when the highest proportion of yearlings was in the active molt remained the same in all three years.

Relationship between seal counts and molt stage

The greatest number of seals in each cohort was counted during the active molt period (Figure 3). The relationships between molt stage proportion and seal counts were generally consistent across years within cohorts (Table 3). The patterns among cohorts were most consistent for the active molt stages (*d-f*), with all cohorts showing a positive relationship between counts and active molt stage proportion. Counts for all cohorts were negatively related to the proportion of seals in stage *a* and *g*, except adult males in stage *g*, which had a small sample size.

DISCUSSION

Cohort differences in timing of molting

We observed the same molting sequence in all three years of our study: yearlings molted first, followed by subadults, then by adult females, and lastly adult males. Thompson and Rothery (1987) found that yearling harbor seals in Scotland molted first, followed by females, immature males, and finally adult males. Although this sequence was somewhat different than what we found, it is not directly comparable because subadult and adult females were grouped together in the Scotland study whereas we grouped male and female subadults together but kept adults separate.

Poor body condition resulting from the annual reproductive cycle may be partly responsible for the later molting period of adults compared to immature seals. Adult females lose a large proportion of their fat layer during lactation and continue to lose fat through the molting period (Pitcher 1986). Although males lose half as much of their blubber layer as females, they begin to lose fat during the mating period and maintain the low fat layer through the molting period (Pitcher 1986). Coltman *et al*. (1997) found that adult males were not feeding during the mating period; instead, they were patrolling for mating opportunities with foraging females. Immature seals may molt before adults because they are not influenced by the energetic demands of the reproductive cycle.

Cohort differences in the timing of molting may also be hormonally influenced (Ashwell-Erickson *et al*. 1986, Thompson and Rothery 1987). Two hormones that may influence timing of molting in immature seals are cortisol, an adrenal hormone, and thyroxine, a thyroid hormone. Cortisol and thyroxine may have antagonistic effects, with cortisol inhibiting and thyroxine stimulating hair growth (Mohn 1958, Riviere *et al*. 1977, Engelhardt and Ferguson 1980, John *et al*. 1987). Immature harbor seals, spotted seals (*Phoca largha*), and grey seals (*Halichoerus grypus*) had low levels of cortisol during rapid hair growth and increased levels of thyroxine during rapid shedding (Ashwell-Erickson *et al*. 1986, Boily 1996). Ashwell-Erickson *et al*. (1986) found no relationship between fluctuations in cortisol/thyroxine levels and the progression of molting in adults and suggested that the effects of reproductive (steroid) hormones in adults may mask the effects of cortisol/thyroxine.

The timing of molting in adult female harbor seals may be influenced by the reproductive cycle due to inhibitory affects of estrogen and the slight stimulatory affect of progesterone on hair growth (Mohn 1958, Ling 1984). Estrogen levels peak at parturition and ovulation, remain low during the period of delayed implantation, and begin increasing again at implantation (Reijnders 1990, Boyd 1991). Progesterone levels peak at parturition, decline sharply during lactation, increase

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after ovulation, and remain elevated throughout delayed implantation (Reijnders 1990, Boyd 1991, Gardiner *et al*. 1999). Molting in adult females coincides with the period of delayed implantation, when estrogen levels are low and progesterone levels are elevated.

Hormonal studies of sexually mature male harbor seals are limited (Gardiner *et al*. 1999). Testosterone is an important hormone in the male reproductive system that may inhibit hair growth (Mohn 1958, Ling 1970). Testosterone is responsible for maintaining primary male sex characteristics, including the production of sperm. Presence of epididymal sperm in sexually mature males was found to bracket the ovulation period of female harbor seals on Tugidak Island (Bishop 1967, Pitcher and Calkins 1979). Most adult males begin molting in late August; we believe this is after most mating occurs on Tugidak Island. Pitcher and Calkins (1979) found no presence of sperm in any seals after October, when most males would have completed the molt. Apparently, the male molting period occurs when sperm abundance is declining and testosterone levels are presumably low.

The hormonal effects of estrogen, progesterone, and testosterone may explain the differences in the timing of molting between adult males and adult females. The presence of these reproductive hormones in sexually mature seals and their absence in immature seals may result in the observed differences in the timing of molting among cohorts.

Cohort differences across years and relationship between counts and molt stage

The timing of molting for all cohorts was nearly identical in 1997 and 1998, but 3-6 days later in 1999 for all cohorts except yearlings, which exhibited no change. The timing of maximal pup counts on Tugidak Island was highly consistent from 1994 to 1998, occurring on 11 or 12 June (Jemison and Kelly 2001), but occurred 4 days later in 1999 (ADF&G unpublished data). The 3-6 day delay in molting among subadults, adult females, and adult males in 1999, combined with later pupping in that year suggests that some common factor(s) influenced those cohorts similarly.

Body condition may have played a role in the timing of molting in 1999. An insufficient fat reserve may cause the body to release stress hormones, such as cortisol, that inhibit hair growth (Mohn 1958, Bullough 1962, Ebling and Johnson 1964, Ling 1984). A depleted fat reserve may be due to changes in food abundance and/or availability. If body condition did influence the timing of molting in 1999, it is unclear why yearlings did not exhibit a delay, unless prey sources for yearlings differ substantially from older seals.

Changes in annual haulout patterns, such as a decreased time spent ashore, may also explain the delayed molting period in 1999. For each cohort, increased seal counts were most closely tied to the active molt period. Seals presumably haul out during the molting period because warmer air temperatures on land allow skin temperatures to be elevated, expediting hair growth (Feltz and Fay 1966). Boily (1995) suggested that harbor seals could molt in water, but haul out to conserve energy because of the energetic expense of maintaining high epidermal temperatures required for mitotic activity. Elephant seals (*Mirounga angustirostris*), grey seals, spotted seals, and harbor seals have a lower resting metabolic rate during the molting period; a decreased resting metabolic rate may help regulate molting by reducing energy requirements and allowing seals to spend more time on shore and less time at sea foraging without a large loss in fat reserves (Ashwell-Erickson *et al*. 1986, Castellini and Rea 1992, Rea and Costa 1992, Worthy *et al*. 1992, Nordoy *et al*. 1993, Rosen and Renouf 1998). If seals had insufficient energy reserves and/or food availability was poor in 1999, they may have spent more time at sea foraging, resulting in slowed mitotic activity and potentially a delay in molting.

Relevance to population monitoring

Population abundance and trend estimates in Alaska are based on aerial counts conducted during the molting period when presumably the largest number of seals are hauled out. The number and sex/age composition of seals counted on shore during the molting period is influenced by cohort differences in molting; thus, surveys conducted during a narrow time window during molting are likely biased toward a certain cohort. In Sweden, the haulout frequency of branded harbor seals differed by cohort throughout the summer, potentially causing sex and/or age biased surveys (Harkonen *et al*. 1999). Differences in the timing of molting among cohorts should be considered when determining optimal survey designs for population abundance and trend estimates.

The timing of pupping varies regionally in Alaska (Bigg 1969, ADF&G unpublished data) and there is evidence that the timing of molting varies regionally as well. In 1998, the date of the maximal count of harbor seals on Tugidak Island occurred on 2 August whereas the maximal counts at Nanvak Bay, in northern Bristol Bay, occurred on 2 September (Jemison & Pendleton 2001*, Jemison *et al*. 2001). A more complete understanding of the spatial variation in timing of molting in Alaska is necessary in order to count seals during the same relative time within the molting period.

Although current statistical models used to estimate population trends take into account the effects of covariates (i.e., time of day, date) on the number of seals on shore, a large temporal shift in the timing of molting within a region could increase variation associated with trend estimates and confound population size estimates. Maximal counts during the molting period were 2-4 weeks later in the late 1970s than in the late 1990s, suggesting a large temporal shift in the molting period (Jemison and Pendleton 2001). In 1976, Johnson (1976) found that only 63% of immature seals had molted by late September yet in 1997 we found that 96% of immature seals had molted by 1 September, providing more direct evidence of a shift in the timing of molting. It is unclear whether this temporal shift in molting was gradual or abrupt. The potential influence of the variation in some of these molt parameters on population survey design are evaluated by Adkison *et al.* (2001).

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Table 1. Classification criteria used to determine molt categories and molt stages for harbor seals on
   Tugidak Island, Alaska 1997-1999.

Molt Category	Molt Stage	% New Hair	Description
Pre-molt	a	0%	overall fading of pelage
	b	0%	pelage bleaching; spots and rings blurring
	c	0%	pelage a uniform tan or brown color; spots and rings not discernable
Active molt	d	25%	isolated patches of new hair on flippers, body openings, head, and scarred tissue
	e	50%	large areas of new hair connect, new hair on dorsal neck region
	f	75%	old hair in isolated patches on dorsum and sides of body
Post molt	g	100%	pelage shiny; spot and rings distinct

Table 2. Estimated dates (95% C.I.) when the highest proportion of each harbor seal cohort was in
the active molt category on Tugidak Island, Alaska 1997-1999.

	1997	1998	1999
Yearlings	2 Aug (2 Aug - 3 Aug)	2 Aug (2 Aug - 3 Aug)	2 Aug (2 Aug - 3 Aug)
Subadults	6 Aug (6 Aug - 7 Aug)	6 Aug (6 Aug - 7 Aug)	12 Aug (12 Aug - 13 Aug)
Adult females	14 Aug (13 Aug - 14 Aug)	14 Aug (13 Aug - 14 Aug)	18 Aug (17 Aug - 19 Aug)
Adult males	28 Aug (25 Aug - 28 Aug)	30 Aug (29 Aug - 1 Sep)	2 Sept (2 Sep - 6 Sep)

Table 3. Slopes, *P* values, and r² for linear regression of counts of each cohort against the proportion in individual molt stages for harbor seals on Tugidak Island, Alaska 1997-1999. *1=intercepts differ among years 2=slopes and intercepts differ among years

	1997			1998			1999			Combined			
Molt Stage	Slope	*P* value	r²	Slope	*P* value	r²	Slope	*P* value	r²	Slope	*P* value	r²	*
Yearlings													
a													
b	29.4	0.835	0.00	-78.9	0.587	0.02	167.6	0.932	0.00	-48.3	0.597	0.16	1
c	-44.0	0.015	0.26	11.2	0.783	0.00	-41.0	0.408	0.04	23.9	0.174	0.19	1
d	145.0	0.000	0.60	230.2	0.000	0.84	65.7	0.072	0.18				2
e	295.9	0.024	0.23	472.6	0.066	0.20	422.2	0.001	0.52	391.0	0.000	0.39	1
f	48.3	0.259	0.06	97.2	0.332	0.06	171.6	0.004	0.40	91.7	0.012	0.25	1
g	-59.2	0.000	0.72	-68.0	0.013	0.33	-44.3	0.036	0.23	-58.4	0.000	0.49	1
Subadults													
a	-555.6	0.139	0.11	-894.8	0.633	0.01				-578.5	0.160	0.17	1
b	-102.2	0.146	0.10	-18.9	0.799	0.00	-178.4	0.020	0.28	-85.7	0.039	0.21	1
c	-34.3	0.361	0.04	-9.9	0.882	0.00	-9.6	0.876	0.00	-16.5	0.577	0.15	1
d	223.0	0.002	0.39	341.2	0.000	0.67	237.4	0.000	0.64	267.8	0.000	0.62	
e	762.5	0.000	0.60	472.6	0.169	0.11	577.3	0.043	0.22	625.5	0.000	0.38	1
f	198.5	0.012	0.28	143.3	0.639	0.05	116.4	0.403	0.04	165.5	0.013	0.23	1
g	-23.3	0.404	0.04	-61.1	0.114	0.15	-47.0	0.240	0.08	-42.2	0.031	0.21	1
Adult Females													
a	-664.9	0.171	0.09	-384.6	0.115	0.18	-516.8	0.012	0.33	-466.0	0.012	0.43	1
b	-17.6	0.891	0.00	82.3	0.630	0.02	-5.8	0.870	0.00	4.5	0.946	0.36	1
c	-35.1	0.941	0.00	1437.7	0.145	0.16	487.3	0.142	0.13	194.7	0.551	0.36	1
d	966.4	0.002	0.38	757.9	0.075	0.22	150.0	0.022	0.27				2
e	1590.4	0.074	0.15	1652.5	0.389	0.06	846.1	0.164	0.11	1519.0	0.011	0.43	1
f	619.2	0.184	0.09	618.8	0.459	0.04	-72.3	0.694	0.01	442.5	0.111	0.39	1
g	-107.3	0.341	0.05	-64.4	0.586	0.02	-42.1	0.281	0.07	-78.9	0.173	0.38	1
Adult Males													
a	-280.7	0.002	0.40	-106.6	0.105	0.20	-255.8	0.018	0.30	-201.3	0.000	0.67	1
b	-193.1	0.021	0.24	19.0	0.844	0.00	-124.1	0.007	0.38	-130.9	0.004	0.60	1
c	-715.3	0.229	0.07	-101.9	0.888	0.00	-201.9	0.445	0.04	-402.9	0.166	0.55	1
d	282.9	0.018	0.25	375.1	0.298	0.09	165.1	0.003	0.41	233.1	0.000	0.64	1
e	1312.7	0.000	0.47	4721.3	0.255	0.11	2183.4	0.049	0.21	1351.7	0.000	0.70	1
f	828.2	0.001	0.43	580.4	0.152	0.16	411.9	0.021	0.28	686.6	0.000	0.69	1
g	434.5	0.001	0.44	93.7	0.215	0.13	328.7	0.033	0.24				2

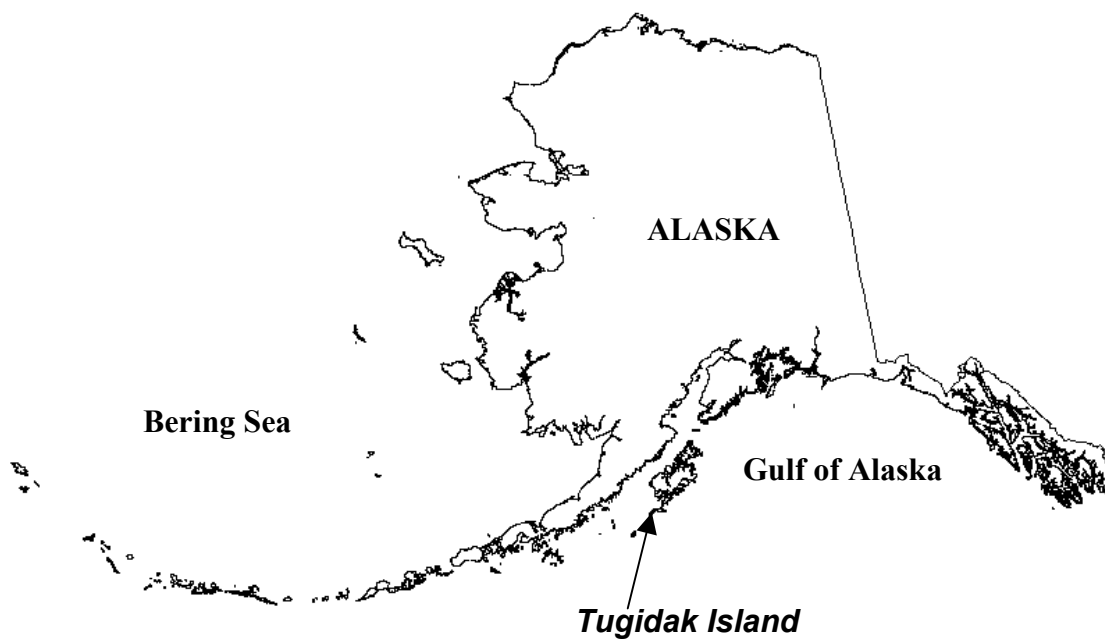ALASKA

Bering Sea

Gulf of Alaska

Tugidak Island

Figure 1.   Tugidak Island, located in the western Gulf of Alaska.

Figure 2. Proportion of harbor seals in the pre (stages *b* and *c* only), active, and post molt periods from 3 July – 15 September, 1998 on Tugidak Island, Alaska; molting curves for the pre, active, and post molt for 1997 and 1999 were similar to 1998.
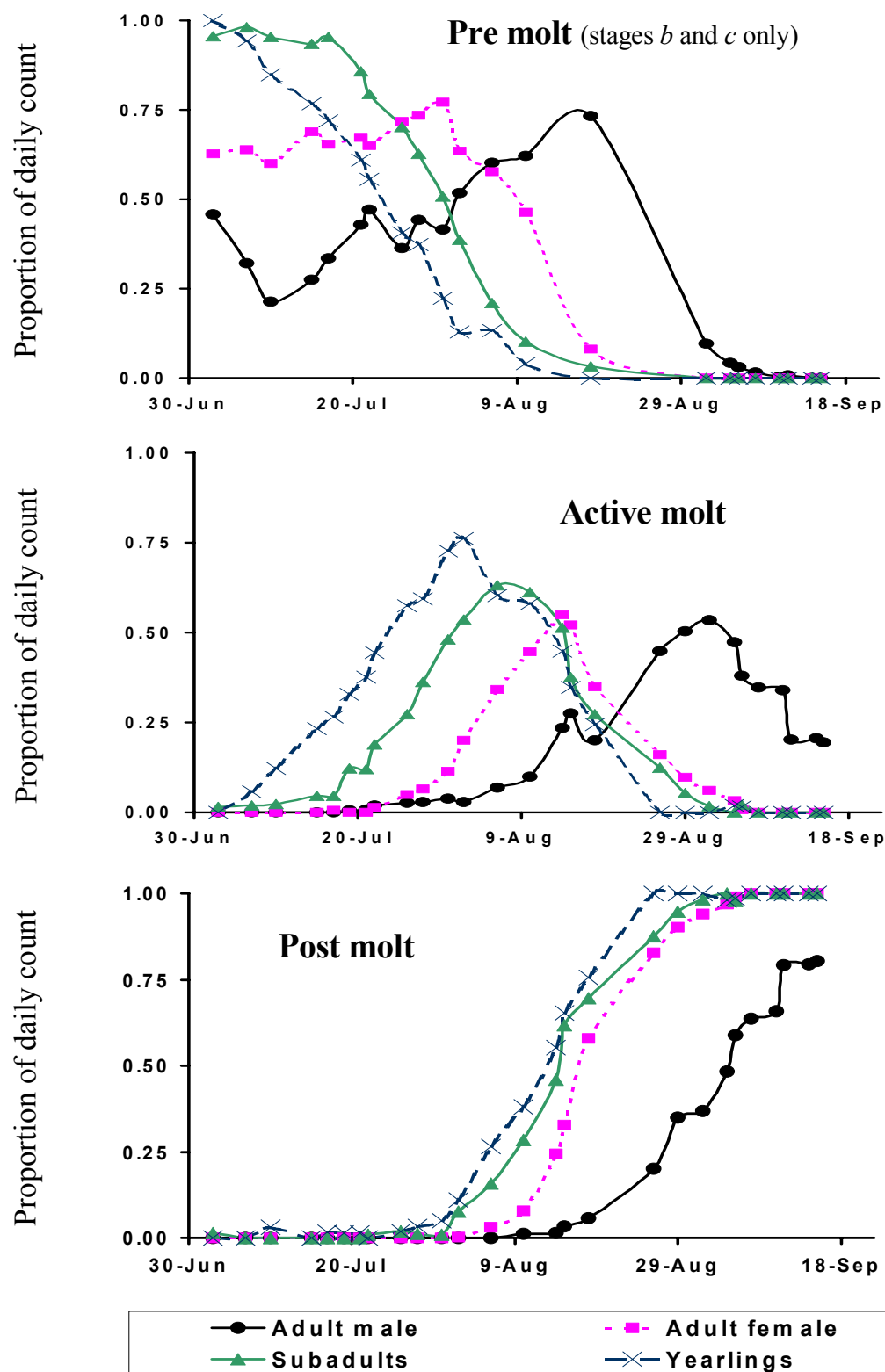
Figure 3. Number and proportion of harbor seal yearlings, subadults, adult females and adult males in molt categories from 3 July – 15 September, 1998, for Tugidak Island, Alaska